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Epizootics and sanitary regulations drive long-term changes in fledgling body condition of a threatened vulture

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ABSTRACT

Epizootics and deliberate changes in policies affecting the environment may affect large groups of species and the functioning of entire ecosystems. Although these effects often overlap in time, their simultaneous effect is rarely examined despite their importance as causes of current biodiversity loss. Here, based on the monitoring of an Egyptian vulture (*Neophron percnopterus*) population over thirty-three years (1986–2018), we increase our knowledge about the effects of anthropogenic-induced changes in food availability, both direct (sanitary policies limiting livestock carcass disposal) and indirect (a wild rabbit epizootic), on brood size and body condition of fledglings at nests. We compared the body mass of fledglings of broods with one chick (*Single*) and two chicks (within which we distinguished *First* and *Second-hatched*). The mass of *Second-hatched* chicks decreased after the plummet in rabbit populations (in the year 1990) and the regulations limiting carcass disposal (2005), reaching minimum values during the period with lowest food availability (i.e. 2005–2013). Recent sanitary legislation allowing carcass disposal by farmers coincides with a slight recovery in the observed body masses. Overall, this study shows that environmental changes of disparate origin can have synergistic effects on individual condition. Conservation of endangered vultures will require multi-targeted conservation plans aimed at ensuring nutritional requirements, in addition to detailed long-term monitoring, in order to detect obscure/masked drivers that affect body condition of fledglings.

1. Introduction

In a scenario of rapid global change, anthropogenic disturbances to populations of vertebrates occur on increasingly shorter-term scales, particularly for large-bodied species (Dirzo et al., 2014). While direct persecution and intentional killing have noticeably declined, at least in developed countries (Deinet et al., 2013), other factors have come into play. Some are unintentional, such as the introduction of invasive species and the spread of epizootics due to globalization, which lead to profound modifications within trophic networks (Millán et al., 2016). Others, however, are triggered by deliberate changes in policies affecting the environment, such as those linked to European agricultural policies which lead to profound and large-scale modifications of habitats, affecting large groups of species and the functioning of entire ecosystems (Donald et al., 2001; Palacín et al., 2018). Although these effects often overlap in time, their simultaneous effects have rarely been examined. Therefore, to curb biodiversity loss, it is imperative that we deepen our knowledge of how the combination of factors from such different sources affect populations, species and ecosystems.

Avian scavengers and vultures in particular, have recently suffered very sharp declines in most of their Old World distribution area, having been extirpated from broad regions (Ogada et al., 2012; Cortés-Avizanda et al., 2016; Buechley and Şekercioğlu, 2016). Where vultures survive, as in Europe, they face serious threats, among which limitation in food availability has a distinct role (Botha et al., 2017). In the last few decades, two processes have radically modified the amount of trophic resources available to these populations in broad regions of the Mediterranean biome. First, at the end of the 1980s, populations of wild rabbits (*Oryctolagus cuniculus*) declined severely after the irruption of Rabbit Hemorrhagic Disease (RHD) (Villafuerte et al., 1995). This harshly affected the cinereous and Egyptian vultures, especially in the Iberian Peninsula (Dobado and Arenas, 2012; Cortés-Avizanda et al., 2015), as well as many

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facultative scavengers (Sebastian-González et al., 2013). Since then, the populations of lagomorphs have recovered irregularly, with many areas still maintaining very low densities thirty years after the arrival of the epizootic (Delibes-Mateos et al., 2014). Second, at the beginning of the 21st century, a drastic reduction in the availability of livestock carcasses occurred as a consequence of the stricter sanitary regulations imposed by the European Union after the irruption of mad cow disease (Donázar et al., 2009). New European legislation, however, meant that from 2011 onwards, farmers were again allowed to abandon livestock remains for avian scavengers at certain sites (Margalida et al., 2012), although these regulations have been irregularly applied by countries and regional administrations, with considerable delays (Arrondo et al., 2018; López-Bao and Margalida, 2018).

Modeling procedures have predicted changes in demographic parameters of European vultures after decreasing food resources following sanitary regulations (Margalida and Colomer, 2012). Field studies also showed a decline in the productivity of Egyptian vultures after the irruption of the wild rabbit RHD (Grande, 2006), and a general reduction in breeding success and survival rates of bearded vultures (Margalida et al., 2014). More fine-tuned adjustments, such as body condition of juveniles at nests, are less likely because vultures, as with other large, long-lived organisms, closely adjust their reproductive efforts to be available trophic resources, with growth variation by means of adjusting the energy requirements of the chicks to limited resources (O'Connor, 1978; Bortolotti, 1986). Research on these topics is important since body condition may be a good predictor of further individual survival (Ronget et al., 2018 and references therein).

Egyptian vultures occasionally raise broods with two chicks (Orta et al., 2019), with the death of second-hatched chicks often occurring soon after hatching (Mendelssohn and Leshem, 1983). Consequently, the surviving chicks show very fixed patterns of growth. If two chicks are raised, both siblings reach similar sizes by flight age (Donázar and Ceballos, 1989) with rare cases of starvation of youngest sibling at this stage. Within this context, and taking advantage of a population-monitoring program for over thirty-three years, we examine long-term trends in body mass of Egyptian vulture fledglings. Our main hypothesis was: that anthropogenically-induced changes in food availability, induced by sanitary policies and the rabbit epizootic, would influence the body condition of fledglings at nests. We specifically compare body masses of fledglings growing in broods of one and two chicks. Because the breeding strategy of large body-sized vultures is extremely conservative (see above) we predicted that changes in fledgling body condition would affect only late hatched chicks, and mainly in those periods characterized by maximum food shortage (reduction in both wild rabbit and livestock carcass availability).

2. Methods

2.1. Study area and field procedures

The study was carried out in the Natural Park of "Bardenas Reales de Navarra" and its surroundings. This area occupies about 50,000 ha of the Ebro Valley, in northern Spain. The area is characterized by a continental Mediterranean climate with less than 300 mm of annual rainfall. The natural vegetation (pine woodland and Mediterranean scrubland) has been largely substituted by pasturelands and extensive cereal cultures. More information on the study area can be found in Cortés-Avizanda et al. (2009, 2015).

This region held a very dense population of Egyptian vultures, with 52 occupied territories at the end of the eighties. The population plummeted to just 20 territories in 2018 (Cortés-Avizanda et al., 2009, 2015; Sanz-Aguilar et al., 2017). Vultures fed mainly on wild rabbits and secondarily on livestock carcasses until the arrival of RHD in 1989–1990. As in other Iberian regions (Delibes-Mateos et al., 2007), the epizootic reduced rabbit populations by around 95%, without subsequent recovery (see Cortés-Avizanda et al., 2015). After the wild rabbit crash, the remains of extensive and intensive farming (sheep, pig and poultry; see Donázar et al., 2010) dominated the bulk of the Egyptian vulture diet in the study area.

Restrictive new sanitary regulations prohibiting the abandonment of livestock carcasses in the field were progressively implemented in Spain from 2001 onwards (Tella, 2001; Donázar et al., 2010; Margalida et al., 2010). Although regulation enforcement showed different intensity across regions, by 2005 it was almost universally implemented in northern Spain, as has been shown in several studies (Camiña and Montelío 2006; Donázar et al., 2010; Margalida and Colomer, 2012; Margalida et al., 2012). It caused the closing of many feeding stations and disposal sites associated with farms, so that in the following years there was a reduction of around 90% in the food biomass provided by livestock carcasses (Margalida et al., 2014). Some regional governments (Navarra, Aragon) created a net of feeding stations trying to alleviate the lack of food (see Arrondo et al., 2018; http://servicios3.aragon.es/bva/i18n/catalogo_imagenes/grupo.cmd?path=3705655), but very few of them are within the potential home ranges of the Egyptian vultures of our study area (see Fig. S1 in Suppl. Mat.). Moreover, large feeding stations are rarely used by breeding Egyptian vultures because they are largely monopolized by dominant griffon vultures (*Gyps fulvus*) (Cortés-Avizanda et al., 2010, 2012). New European regulations (CE 322/2003, and specially CE 830/2005 CE 142/2011) were put in place to reverse this scenario, and were applied progressively by states and regional administrations (see Margalida et al., 2012; Mateo-Tomás et al., 2019). In the study area, the regulations were applied from 2013 in Aragón (D. 170/2013) and from 2014 in Navarre (OF 46/2014). It allowed farmers to maintain small feeding points near their farms. The implementation of these regulations has been much more developed in Navarre (the main part of the study area) whereas they have been embraced only by a few farmers in Aragon (M. Alcantara pers. Comm.1st September 2019). In the meanwhile, the disposal of carcasses and other remains from intensive farming (pigs and poultry) are still prohibited, although illegal disposal occurs.

From 1986 to 2018, we carried out detailed annual monitoring of the population, including the assessment of breeding success in each territory and the marking of fledglings at nests (see details in Sanz-Aguilar et al., 2017). Fledglings were marked with plastic and metal rings at the end of the development period, when they were between 45 and 65 days old (and in rare cases, at a younger age). At this age, prospects of survival of the young are very high (Donázar and Ceballos, 1989). From 2005 to 2009, because of limited funds, the chick marking was stopped, the study being resumed in 2010. For each fledgling, we recorded the body mass (in grams) and the length of the seventh primary feather (in mm). It has been previously demonstrated that the primary feather length is a good predictor of the age of the chicks because its growth rate is only affected by extreme starvation. Therefore, we used this measure as a proxy of fledgling age (Donázar and Ceballos, 1989).

3. Analytical procedures

Because Egyptian vultures may raise broods of one or two fledglings (see above), we separately modeled long-term changes in body mass of the fledglings growing alone (hereafter "*Single*"), first-hatched chicks of broods of two ("*First-hatched*") and second-hatched chicks of broods of two ("*Second-hatched*"). Following Sánchez-Montoya et al. (2016) (see also Zuur et al., 2009), we fitted Generalized Linear Mixed Models (GLMM) including "*Territory*" as a random term. In the three analytical trials, the response variable was "*Body mass*". Three explanatory variables were considered: feather length, period and hatching date. Feather length of the seventh primary "*Primary*" was fitted as a co-variable to account for the age (size) of the birds (García-Berthou, 2001; Paquette et al., 2014). We discarded data from those chicks less than 45 days old to avoid non-normality distributions in weight. Period of study "*Period*" was fitted according to the abovedescribed large-scale and long-term changes in food availability. Thus, we considered the following four levels for *"Period"*: 1) 1986–1989. High wild rabbit abundance, prior to the decline of rabbit populations due to the spread of RHD in the study area; 2) 1990–2004. Low wild rabbit abundance but still high availability of livestock carcasses because of the absence of applied sanitary regulations; 3) 2005–2013. Low wild rabbit abundance and low availability of livestock carcasses because of the implementation of sanitary regulations; 4) 2014–2018. Low wild rabbit abundance and moderate availability of livestock carcasses because of the implementation of less restrictive sanitary regulations. It should be noted that we lack of information on fledgling body condition from 2005 to 2009, so the period over which data is actually analyzed is 2010–2013. However, as we have information on brood size for all years, we have chosen to keep the "2005–2013" label for this period.

Date of hatching "*Hatching date*" was fitted because young birds born early in the season may experience better conditions during growth (Catry et al., 2017). Julian hatching date (1 = 1st of May) was estimated by backdating from the age of birds at ringing (estimated from the length of the seventh primary, see above). Comparisons between competing models were based on the small-sample-size corrected version of the Akaike information criterion (AICc, Burnham and Anderson, 2002) after excluding models with uninformative parameters (Anderson, 2008; Arnold, 2010).

Statistical procedures were carried out in R 3.02 (R Core team, 2016) using the packages *lme4* (Bates et al., 2015) and *MuMIn* (Barton, 2017). Post-hoc comparisons between "Period" levels were done with the package *multcomp* (Hothorn et al., 2008).

4. Results

Between 1986 and 2018, we recorded 494 broods of Egyptian vultures, of which 294 had a single chick and 200 had two siblings. This yielded a total rate of 1.41 fledglings per successful brood. This rate varied along the study period and was slightly higher (3–7%) in the two first periods of monitoring (i.e. 1986–1989: 1.42 and 1990–2004:1.44) with respect to the rest (i.e. 2005–2013: 1.33; and 2014–2018: 1.38) but the differences between periods were not significant (Chi-square = 3.799, d.f. = 3, p = 0.284) (see Fig. 1).

The comparison of the competing models revealed that for "*Single*" and "*First-hatched*" chicks the most plausible model included only the variable "*Primary*" (Table 1), indicating that the body mass of these chicks increased linearly with age (Fig. 2). The following models with similar values of AICc (in both cases *Hatching date* + *Primary* and *Period* + *Primary*; Table 1) all

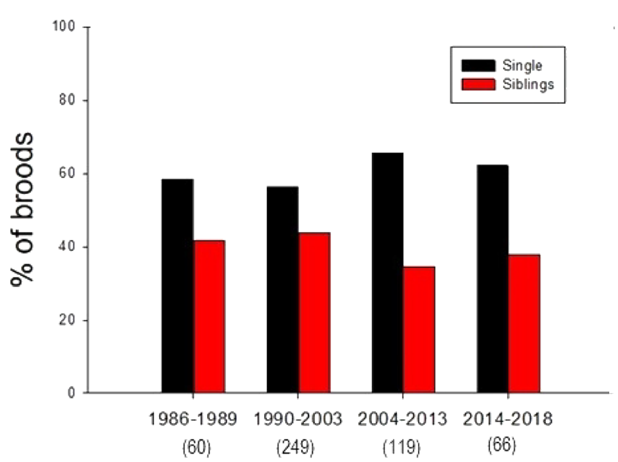

Fig. 1. Changes in the frequencies of broods with single chicks and siblings during the four periods of monitoring. Sample sizes are shown in brackets. The frequencies did not differ between periods (Chi-square = 3.799, d.f. = 3, p = 0.284).

Table 1
Competing GLMMs examining the effect of *Hatching date*, *Period* and *Primary* on fledgling body mass of Egyptian vultures. *Territory* was fitted as a random term. Models were separately fitted for single (brood of one), first-hatched and second-hatched chicks (broods of two). d.f. = degrees of freedom; Delta_AICc = Difference in AICc between each model and the top-raked one; AICcWT = AICc weight; Cum.Wt: Cumulative AICc weight.

Model	d.f.	AICc	Delta_AICc	AICcWt	Cum.Wt
Single					
Primary	4	2048.1	0.00	0.673	0.673
Hatching date + Primary	5	2050.2	2.13	0.232	0.905
Period + Primary	7	2052.7	4.64	0.066	0.971
Hatching date + Period + Primary	8	2054.7	6.60	0.025	1
Null	3	2059.2	11.19	0.002	1
Hatching date	4	2060.8	12.77	0.001	1
Period	6	2063.6	15.56	0.000	1
Hatching date + Period	7	2065.6	17.51	0.000	1
First-hatched					
Primary	4	1704.4	0.00	0.556	0.556
Hatching date + Primary	5	1706.1	1.72	0.235	0.795
Period + Primary	7	1706.9	2.53	0.156	0.951
Hatching date + Period + Primary	8	1709.2	4.78	0.051	1
Hatching date + Period	7	1716.9	12.49	0.000	1
Period	6	1718.0	13.59	0.000	1
Null	3	1718.9	14.44	0.000	1
Hatching date	4	1720.2	15.78	0.000	1
Second-hatched					
Period + Primary	7	1745.7	0.00	0.427	0.427
Hatching date + Period + Primary	8	1746.9	1.18	0.237	0.664
Hatching date + Primary	5	1747.5	1.73	0.180	0.844
Primary	4	1747.8	2.03	0.155	1
Hatching date + Period	7	1780.9	35.18	0.000	1
Hatching date	4	1783.2	37.51	0.000	1
Period	6	1789.1	43.33	0.000	1
Null	3	1791.0	45.24	0.000	1

included uninformative parameters (95% confidence interval overlapped zero). The procedure for "*Second-hatched*" chicks revealed three highest-ranked models including combinations of the variables *Period*, *Primary* and *Hatching date*, but only the first model retained informative parameters (Table 1). The fourth model (including only *Primary*) was at 2.08 delta AIC points and was about two- thirds less supported according to AICc weights. The summary of the first model (Table 2) revealed a positive effect of the primary feather length (age) and a negative estimate for the period with the lowest food availability (i.e. 2005–2013) and, to a lesser extent, for the period 2014–2018. Post-hoc Tukey tests revealed significantly higher body masses for the period with highest food availability (1986–1989) in relation to 2005–2013 and, to a lesser extent 2004–2018 (Fig. 2).

5. Discussion

Our results show that according to our main hypothesis, long-term variations in trophic resource availability did not affect the brood size but the body condition of Egyptian vulture fledglings. We also predicted, there were differences in relation to hatching order, so that second-hatched chicks, but not first-hatched or single chicks, were affected. The resulting model for second-hatched chicks accounted for an important proportion of the variance (Table 2). This finding is notable since, as stated above, growth patterns of the study species were very consistent in years of high availability of resources (Donázar and Ceballos, 1989). In these conditions, chick casualties in large body-sized vultures due to starvation are extremely rare, with most of the losses caused by adverse weather and human disturbance in early stages (Arroyo and Razin, 2006; Zuberogoitia et al., 2008; Blanco et al., 2017).

The decrease appeared when the decline in European wild rabbit populations and veterinary sanitary regulations were added. While the severe decline in European wild rabbit populations had consequences on breeding success (Grande, 2006), it did not seem to affect the body

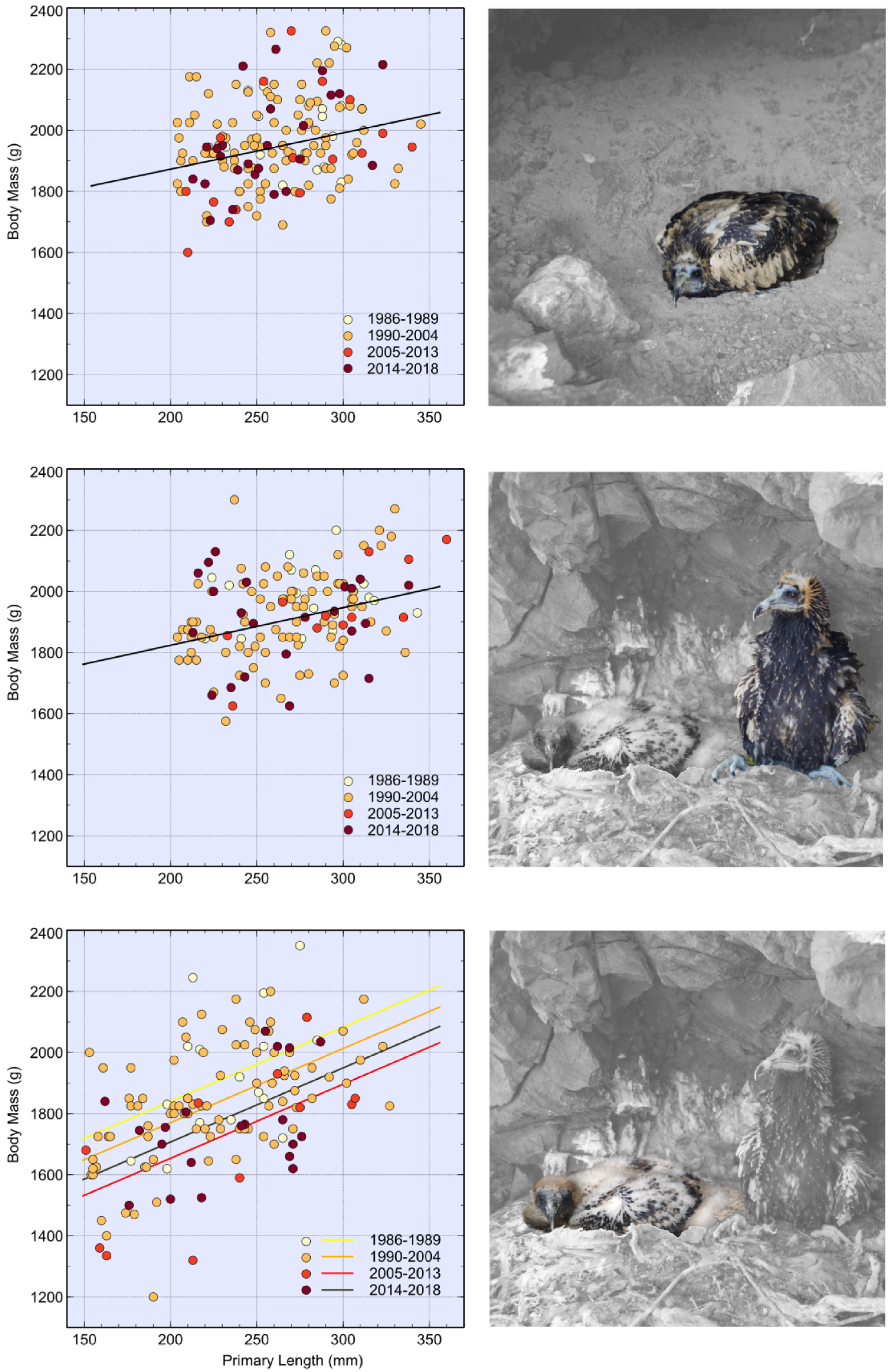

Fig. 2. Variation in the relationship between body mass and length of the seventh primary of fledgling Egyptian vultures disaggregated by the four periods of monitoring. *Single* (broods with one chick), and *First-hatched* and *Second-hatched* (broods with two chicks) fledglings are distinguished. Fitted lines from the resulting models are also shown.

Table 2
Summary results of the most parsimonious models fitted for single, first-hatched and second-hatched fledglings. R^2m and R^2c represent respectively the marginal and the conditional (with random effects) r-squared.

	Estimate	Std. Error	t value
Single			
Intercept	1645.1704	86.9105	18.929
Primary	1.2285	0.3303	3.179
R^2m	0.0747		
R^2c	0.2304		
First-hatched			
Intercept	1610.7656	77.4515	20.797
Primary	1.1725	0.2814	4.167
R^2m	0.09878		
R^2c	0.3567		
Second-hatched			
Intercept	1355.2135	87.7304	15.447
Period: 1990–2004	−69.7653	45.5932	−1.530
Period: 2005–2013	−186.3917	65.8576	−2.830
Period: 2014–2018	−133.0936	56.9039	−2.339
Primary	2.4252	0.3289	7.374
R^2m	0.31176		
R^2c	0.3987		

condition of nestling Egyptian vultures on its own. In the years after the European wild rabbit population crash, livestock numbers were still high and the abandonment of remains was still unregulated, such that vultures could find food in areas neighboring the Natural Park (Cortés-Avizanda et al., 2015).

The situation changed radically after the new and restrictive sanitary regulations were implemented from 2004 onwards due to the bovine spongiform encephalopathy (BSE) crisis. At that point, clear negative effects on the mass of the younger siblings of broods of two chicks were detected (Table 2). Other factors indirectly associated with the reduction of trophic resource availability cannot be ruled out as potentially contributing to these effects. We know that the non-natural mortality of territorial Egyptian vultures, mainly due to incidental poisoning, increased in the study area after the European wild rabbit crash led to the use of more developed foraging areas (Cortés-Avizanda et al., 2009, 2015). A higher rate of adult bird turnover implies the recruitment of less experienced birds with fewer skills in searching for trophic resources (Margalida et al., 2011). This fact, in addition to further reductions in the availability of carcasses due to sanitary regulations, could result in a less experienced, rejuvenated population relying on vanishing trophic resources.

The recovery of the body condition of second-hatched chicks after authorization to abandon livestock carcasses was apparent but estimates overlapped with those observed in the previous period (Table 2). Reasonably, the amount of livestock carcasses is still less than before the total interdiction. It is still forbidden to dump carcasses from intensive farming, mainly poultry and pig farming, although this occurs illegally with relative frequency (authors' unpublished observations). Moreover, although the disposal of carcasses from extensive farming has been authorized in the neighboring region of Aragon since 2013, where the Egyptian vultures of the Park habitually forage (Cortés-Avizanda et al., 2015) only a few dumping points exist and all distant to the study area (Fig. S1). This again highlights the problem inherent to unequal implementation of sanitary policies between neighboring administrations (Arrondo et al., 2018; López-Bao and Margalida, 2018). In addition, the European wild rabbit population, formerly extremely abundant in the Natural Park and its neighboring areas, has not recovered from the crash in the 1980s (Bardenas Reales Natural Park, unpublished data).

The impact on second-hatched chicks of relatively low body condition after they leave the nest remains unknown. It is recognized that individuals subject to harsh food conditions in the nest can experience lower post-fledgling survival (Naef-Daenzer et al., 2001; Briga et al., 2017). Survival studies carried out up to 2004 in the same study area revealed that there was no effect of body mass on the survival probability of fledgling Egyptian vultures (Grande et al., 2008). However, that study did not include data beyond the implementation of sanitary regulations. In light of the current results, however, it would be desirable to assess whether the relatively lower availability of food resources during the last decade has had any impact on survival, as well as on other life-history traits like adult body size, acquisition of breeding territories and fecundity (see review in Metcalfe and Monaghan, 2001).

Whether or not the current scenario is reversible remains uncertain. As we stated above, the recovery of the European wild rabbit population seems, for the moment, unlikely in the study area, even more so given a new viral disease that appeared in the Iberian Peninsula in 2012–2013, increasing European wild rabbit mortality (Abrantes et al., 2013; Delibes-Mateos et al., 2014). Additionally, land abandonment may, in the medium- and long-term, lead to the weakening of extensive grazing and the loss of Mediterranean cultural landscapes where European wild rabbit populations found an appropriate habitat (García-Barón et al., 2018). Moreover, extensive and semi-extensive livestock sheep husbandry are in decline, as they are being substituted by intensive pig and poultry farming (Bernués et al., 2011) whose sub-products are not permitted to be abandoned for avian scavengers. These remains are unsafe for feeding vultures because of the increasing probability of pathogen transmission as well as ingestion of pharmaceutical drugs (Blanco et al., 2016, 2017; Blanco, 2018).

Our findings highlight that the growth patterns of the studied population of vultures, which had previously been nearly invariable, have been seriously affected by the synergistic effect of food constraints from disparate sources, including epizootics and sanitary policies. Conservation of Egyptian vultures and other avian scavengers will require multi-target conservation plans aimed at ensuring varied food sources (wild prey, extensive livestock) providing both qualitative and quantitative nutritional requirements (Mateo-Tomás and Olea 2010; Dupont et al., 2012; Cortés-Avizanda et al. 2016; Botha et al., 2017). In addition, we highlight the need for long-term monitoring of endangered long-lived species (Perrig et al., 2019), with particular scrutiny of potentially hidden effects within parameters that show apparent stability such as the fledgling rate from successful nests.

Authors' contributions

Conceived and designed the study: JAD & ACA. Field-work: JAD, ACA, OC, DS, JMG EA. Compiled the data, prepared data and performed analyses: JAD, OC, ACA. Writing of the manuscript: all coauthors.

Declaration of interest statement

None.

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Appendix A. Supplementary data

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